The Plant Photobiology Notes 1

Light signals and the growth and development of plants — a gentle introduction

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Draft of April 2006

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Draft printings:
First: October 1999 (Joensuu)
Second revised: May 2001 (Joensuu)
Third revised: July 2005 (Jyväskylä)
Fourth revised: April 2006 (Jyväskylä and Helsinki)

Typeset with LaTeX.
Edited with WinEdt.

Dedicated to Professor Rodolfo A. Sánchez

Preface

A recent article in the journal *Natural History* was titled 'How plants "see"' (Yanovsky and Casal, 2004). Yes, plants have a kind vision, although very different to that of animals. This sense of vision in plants is what I describe in this notes. Not only how it works (the physiology) but also its apparent function in plant adaptation (why has it evolved through natural selection?).

The sections in these notes follow a sequence that starts with a description of the environmental signals in natural light, and progresses towards ecological implications. In section 1 I introduce the basic concepts of photochemistry, photobiology, photosensory biology, and how plants interact with their light environment. In section 2 I discuss the nature and origin of light signals —signals that carry information about the abiotic and biotic environment that are potentially useful to plants. In section 3 I describe the different photoreceptors that have been identified in plants, and summarize what is known about their functions and localization. In section 4 I briefly present some examples of how the signal sensed by the receptors in transduced within the cells. In section 5 I give several examples of responses to light in whole plants. In section 6 I discuss the implications of the responses of individual plants for the behaviour of plant canopies and populations. I also consider the question of whether sensory responses to light are adaptively beneficial to plants. In section 7 I attempt to guess at the future and list some ideas about the limitations of current state of knowledge. Finally, in section 8 I give a link to a list of further reading for those willing to go in greater depth into the sensory photobiology of plants.

Acknowledgements: These notes started to take shape slowly about ten years ago, and finally took shape during my participation as a teacher in a plant photobiology course organized at the University of Joensuu. While in Joensuu, I still updated them once. In 2005 I participated in environmental science field course organized at the University of Jyväskylä, and did a much needed partial update. The current version is a further update for the ecology field course at the University of Helsinki, done while still working at the University of Jyväskylä.

Caveat: These notes are still a draft. They are incomplete and not totally up-to-date. I have taken many of the examples from my own work, because I had the illustrations available, and because being my own work, I did not need to ask for permission to reproduce them. In other words, I did not choose them on the base of scientific priority, but instead mainly to avoid dealing with copyright permissions. Of course, I used those examples that I thought led to clearer explanations.

I hope that you find these notes useful and entertaining, even though they are still work in progress.

Jyväskylä, April 2006.

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1 Introduction

1.1 What is light?

Light is electromagnetic radiation of wavelengths to which the human eye is sensitive ($\lambda \approx 400$ to 700 nm). However, sometimes the word *light* is also used to refer to other nearby regions of the spectrum: ultraviolet (shorter wavelengths than visible light) and infra-red (longer wavelengths).

Both particle and wave attributes of light are needed for a complete description of its behaviour. Light particles or quanta are called photons. The energy possessed by one photon or quantum depends on the frequency (or colour):

$$E_\lambda = h\nu = hc/\lambda_{\text{vacuum}} \tag{1}$$

where E_λ is a quantum, or the amount of energy that one photon has, h is Plank's constant, ν is frequency, λ is wavelength, and c is speed of light in vacuum.

The units used for describing light intensity depend on whether quanta or energy are measured, and on the geometry of the sensor (Table 1). Light flux measured as energy received on a flat surface, per unit area and per unit time is called *irradiance*. Light flux as received on a spherical surface and per unit time is called *fluence rate*. The total amount of light received per unit area (i.e. irradiance integrated over time) is called *fluence*. The total amount of light absorbed per unit area (e.g. fluence multiplied by the receiving body's absorptance) is called *dose*. *Energy* and *photon* units can only be converted into each other with knowledge of the light spectrum, because as described by equation 1, the energy carried by one photon depends on its wavelength.

Table 1: Quantities commonly used for expressing light measurements. Energy is implied when omitted, photon should be always explicitly indicated. *Photon flux density* is sometimes used as a synonym for photon irradiance.

Geometry	Instantaneous values		Time integrated values	
	Energy system	Photon system	Energy system	Photon system
Flat	(energy) irradiance	photon irradiance	time integrated (energy) irradiance	time integrated photon irradiance
Spherical	(energy) fluence rate	photon fluence rate	(energy) fluence	photon fluence

1.2 Principles of photochemistry

Sensing of light by plants and other organisms starts as a photochemical event, and is ruled by the basic principles of photochemistry:

Grotthuss-Drapper law Only light that is actually absorbed can produce a chemical change.

Stark-Einstein law Each absorbed quantum activates only one molecule.

Einstein postulate All energy of the light quantum is transferred to a single electron during the absorption event.

As electrons in molecules can have only discrete energy levels, only photons that provide a quantity of energy adequate for an electron to 'jump' to another possible energetic state can be absorbed. The consequence of this is that substances have colours, i.e. they absorb photons with only certain energies.

1.3 What is photobiology?

Photobiology is that branch of biological science which studies the interactions of light with living organisms.

It includes photomedicine, photosynthesis, environmental photobiology and photosensory biology. In this note, however we will only consider the photosensory biology of plants.

1.4 Plant photosensory biology

Photomorphogenesis. Nature has produced a number of light-absorbing molecules that enable organisms to respond to changes in the natural light environment. Light signals can regulate changes in structure and form, such as seed germination, leaf expansion, stem elongation, flower initiation and pigment synthesis. These photomorphogenic responses confer an enormous survival advantage on organisms.

Chronobiology. The ability to distinguish time of day without reference to external light or darkness is found in both plants and animals. Light has important effects on this time sense, or circadian clock, as it is sometimes called. Light keeps the timing cycle synchronous with day and night, adjusts it to long or short days, and even stops or starts it under certain conditions (a phenomenon called photoperiodism).

Photomovement. Photomovement involves any light-mediated behaviour that results in movement of an organism. A common example is the bending of plants toward a light source (a phenomenon called phototropism). Such responses depend upon the organism being able to determine the intensity and direction of light.

1.5 Plants and their light environment

A complete description of the light incident on a plant requires the characterisation of its intensity (photon or energy irradiance), duration, quality (spectral composition), and direction (relative location of source, and degree of scattering).

Light is both a source of energy and a source of information for green plants. It is a source of energy for photosynthesis, and a source of information for photoperiodism (night/day length), phototropism (light direction), and photomorphogenesis (light quantity and quality).

Plants both affect and are sensitive to light quality and quantity (see Aphalo and Ballaré, 1995, and references therein). In other words plants both generate and perceive light signals. Several photoreceptors are involved in the perception of these signals which are used by plants to gather positional and size information about other plants which are near them —i.e. about their

neighbours. The sensitivity of plants to light provides them with the sense of *vision*, although a very different kind of vision than that provided by the eyes of humans and animals.

Other environmental signals, not related to neighbours, are dark/light transitions such as those occurring at the soil surface, and those related to day/night length. Photoreceptors are also involved in the perception of these signals.

The main informational photoreceptors in plants can be classified into three groups: phytochromes, blue/UV-A and UV-B photoreceptors. Phytochromes exist mainly in two interconvertible forms, one with maximum absorption in the red (peak at 660 nm) and another with maximum absorption in the far-red (peak at 730 nm), and are capable of sensing both irradiance and the photon ratio between the red and far-red portions of the spectrum. Blue/UV-A and UV-B specific photoreceptors absorb light in different regions of the light spectrum and sense irradiance.

Responses of plants to light quality and quantity can be studied at different scales. At the subcellular level the best characterised response is altered gene expression, but other possible pathways for action are transient changes in membrane permeability and modulation of the activity of specific enzymes.

Whole plants respond to shading and/or neighbours with increased stem elongation rates, increased area of individual leaves, altered shape of leaf blades, more horizontal leaf blades, and more vertical stems, branches or tillers, increased apical dominance, changes in chemical composition (mineral nutrients, anthocyanins, chlorophylls and other metabolites). Light is required for the germination of many seeds, and is also involved in de-etiolation[1] of seedlings emerging through the soil surface.

In a canopy, either closed or sparse, plants adjust their growth and development in response to their sensing of neighbouring vegetation. The responses to alterations in light quality produced by neighbours can occur even before any shading takes places. The "shade-avoidance" response decreases the size variability between individuals in a canopy and causes a more even sharing of resources between individuals —i.e. photomorphogenic responses can **increase** the uniformity of plants growing within a canopy. Another response to light quality is the timing of seed germination.

2 The light signals

2.1 The solar spectrum

Sunlight (direct beam) has a more or less continuous spectrum in the visible, infrared and ultraviolet-A range (Fig. 1). In this range the spectrum is similar to the emission spectrum of a black body at 5800 K, except for a few valleys caused by absorption bands of water, oxygen and carbon dioxide. Ultraviolet-B radiation is partly absorbed by ozone in the atmosphere, while ultraviolet-C is totally absorbed. Skylight (diffuse radiation) is richer in blue and shorter

[1] The transition from darkness under the soil to exposure to white light after emergence initiates de-etiolation: hypocotyl growth slows down or stops, cotyledons expand and unfold, the apical hook opens, gene expression changes.

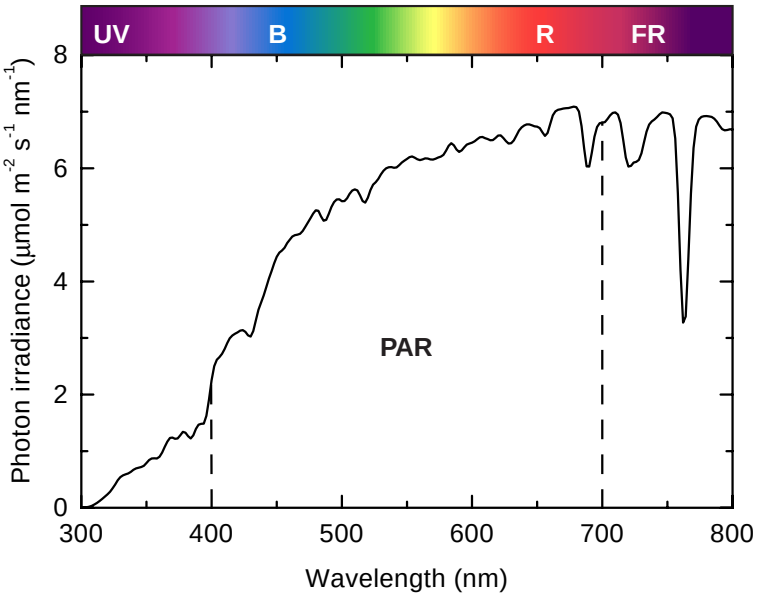

Figure 1: The solar spectrum at the earth surface. Measured near noon with a cosine corrected light collector pointing at the solar disc, in the summer at 63^0 N (Pedro J. Aphalo, unpublished).

wavelength radiation which are more affected by molecular scattering than radiation of longer wavelengths. The peak of the sunlight spectrum shifts towards red (longer wavelength) when the sun is at a low elevation angle (near the horizon).

2.2 Visible light

When light impinges on a leaf, some of it is reflected, some is transmitted and the rest is absorbed (Fig. 2). Light of different wavelengths is affected differently. Reflected and transmitted light is scattered (as opposed to mirror reflection). Absorptance in the "photosynthetically active range" (400 nm to 700 nm) is very high in young fully expanded leaves (80% to 95% of the incident light) (Fig. 3). Leaf surfaces that look very dark such as the adaxial (upper) epidermis of ivy (*Hedera helix*) leaves have low reflectance (less than 10%) even in the green region of the spectrum. The abaxial (lower) epidermis of ivy leaves and both epidermes of other species such as birch can reflect as much as 20% of the green light in sunlight and look green. Transmittance is also higher in the green than in other bands of the visible spectrum and because of this, leaves also look green when light shines through them. Far-red light is not absorbed by leaves, approximately half of it is reflected and the rest is transmitted (and scattered).

As not only leaves and cotyledons, but also growing internodes and hypocotiles can sense the light environment, the quality of light incident on both horizontal and vertical surfaces is significant for plants.

In the understorey of forests or under a dense canopy of herbaceous vegetation the effect of

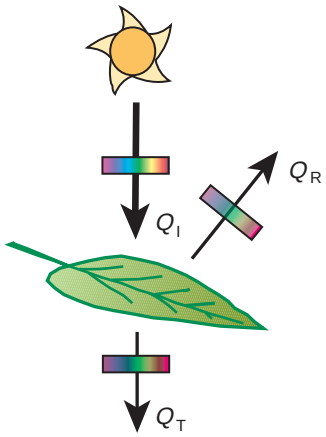

Figure 2: Interaction of sunlight with a leaf. Incident light is partly reflected, transmitted and absorbed. Reflected and especially transmitted light is strongly scattered.

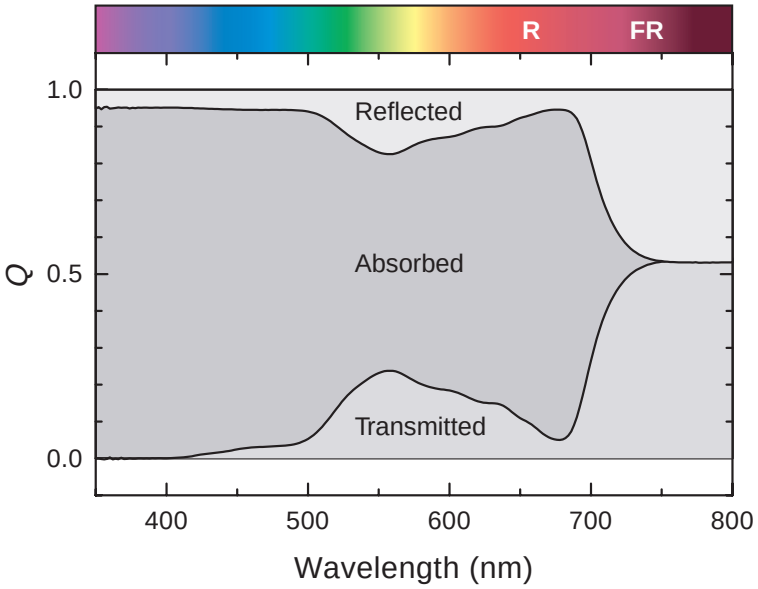

Figure 3: Transmittance, reflectance and absorptance of the adaxial surface of a young fully expanded leaf of a silver birch (*Betula pendula* Roth.) seedling (Pedro J. Aphalo and Tarja Lehto, unpublished).

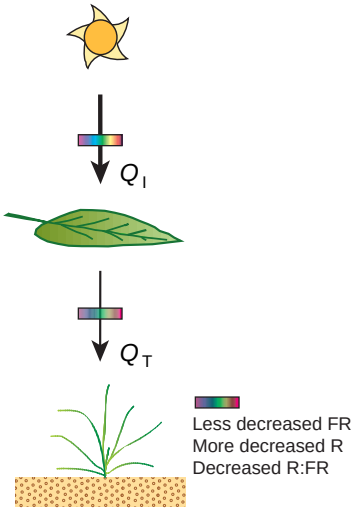

Figure 4: Interaction of sunlight with foliage: transmitted far-red (FR) light and "understorey" vegetation.

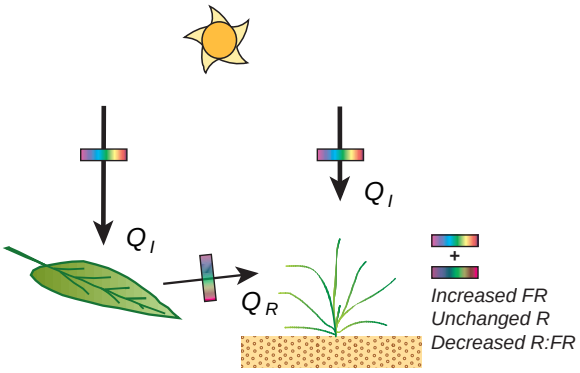

Figure 5: Interaction of sunlight with foliage: reflected far-red (FR) light and "neighbouring" vegetation.

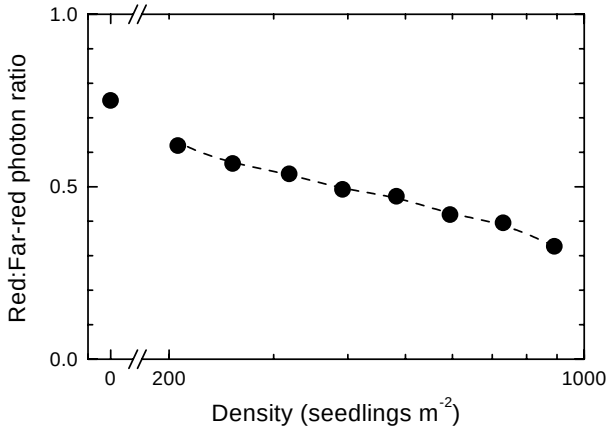

Figure 6: Red to far-red photon ratio (R:FR), of the horizontal flux of radiation within a canopy, as a function of the density in a canopy of young birch seedlings. The canopy layout was a Nelder 'cartwheel'. A cylindrical light collector attached to red and far-red light sensor was used. Values are means of four replicate canopies (From Aphalo et al., 1999).

light absorption predominates: blue, red, and to a slightly lesser degree green light are strongly attenuated, while far-red light is moderately attenuated (Fig. 4). This is a classical setting for the discussion of the role of phytochromes, which can sense the red to far-red photon ratio (R:FR). R:FR, measured on a horizontal surface, is about 1.12 in sunlight and can be as low as 0.01 under a closed canopy (see Smith, 1994).

In a sparse canopy (e.g. leaf area index (ratio of leaf area to ground area) of less than unity) there is almost no shading between plants during most of the day. Under these conditions the effect of reflectance predominates: light near neighbours becomes enriched in far-red without much change in the blue, green or red bands (Fig. 5). This is especially noticeable when what is measured is the horizontal (mostly scattered) light flux. R:FR, measured on a vertical surface, is about 0.75 in an open place or above the vegetation, and decreases as a function of the density of the canopy (Fig. 6). At low plant densities the main effect is an increase in far-red light with no decrease in red, at higher densities red light decreases more than far-red light (Aphalo et al., 1999; Ballaré, 1999).

2.3 UV-B radiation and stratospheric ozone

Plant responses to UV-B are important on two accounts: (1) the recent anthropogenic increase in UV-B irradiance at ground level, especially at high latitudes (Madronich et al., 1995) , and (2) the normal seasonal and spatial variation in UV-B irradiance. The increase in the UV-B irradiance is caused by the depletion of the ozone layer in the stratosphere, mainly as a consequence of the release of chlorofluorocarbons (CFCs). The most dramatic manifestation has been the seasonal formation of an "ozone hole" over Antarctica. It is controversial whether a true ozone hole has already formed in the Arctic, but atmospheric conditions needed for the formation of a "deep"

ozone hole are not very different from those prevalent in recent years. Not so dramatic, but consistent, depletion has also been observed at middle latitudes in both hemispheres. As CFCs have a long half life, of the order of 100 years, their effect on the ozone layer will persist for many years, even after their use has been drastically reduced. Normal seasonal and spatial variation can also be sensed by plants, and could play a role in their adaptation to seasons and/or position in the canopy.

3 The photoreceptors

Pigments are molecules that absorb light (usually in the range 320 nm to 760 nm). By absorbing photons these molecules become excited. This excitation energy can then be re-emitted as light (luminescence), thermally dissipated, or transferred to other molecules. But most importantly the energy in the absorbed photons can drive chemical transformations, such as electron transfer, phosphorylation or conformational changes.

Pigments can be classified into two main groups: (1) Those for which the amount of energy absorbed is a relatively large fraction of incident light, called *mass pigments* because they are in relatively high concentrations in plant tissues. (2) Those pigments which only absorb a small fraction of the incident light, called *sensor pigments*.

Pigments from the first group either absorb photons which drive metabolic processes (i.e. they 'harvest' energy) like chlorophylls, or absorb potentially damaging photons (i.e. they 'screen' light away from sensitive tissues) like anthocyanins and flavonoids, and by dissipating this energy safely afford protection to other cell components. Pigments (e.g. in flowers) can also be signals involved in interactions with animals (e.g. pollinators).

Pigments from the second group sense (i.e. 'gather' information about) the light environment. The function of these pigments is to adjust the developmental program and behaviour of plants to the prevailing environmental conditions (e.g. seasons and location). These pigments are red/far-red- (phytochromes), blue/UV-A- (cryptochromes and phototropins) and UV-B- photosensors or photoreceptors. The molecular and spectral characterisation of these light sensors has advanced quickly in recent years (see Batschauer, 1998).

3.1 Phytochromes

Phytochrome photoreceptors are present in higher plants (gymnosperms, angiosperms) and lower plants (ferns, liverworts). They are almost certainly ubiquitous in green plants (Mathews and Sharrock, 1997). Recently, a phytochrome has been found in the cyanobacterium *Synechocystis* (Hughes et al., 1997), however, in most lower organisms light is detected by other photoreceptors.

Phytochromes are a family of soluble dimeric proteins with a tetrapyrrole chromophore. They probably function without being bound to a membrane. The monomer consists of an apoprotein (molecular weight of 120 kDa to 130 kDa, depending on the specific phytochrome) which is linked to an open-chain tetrapyrrole chromophore.

Phytochromes are photochromes (pigments that change colour when they absorb light): each phytochrome (P) can exist in two relatively stable forms, P_r and P_{fr}, which differ in their chro-

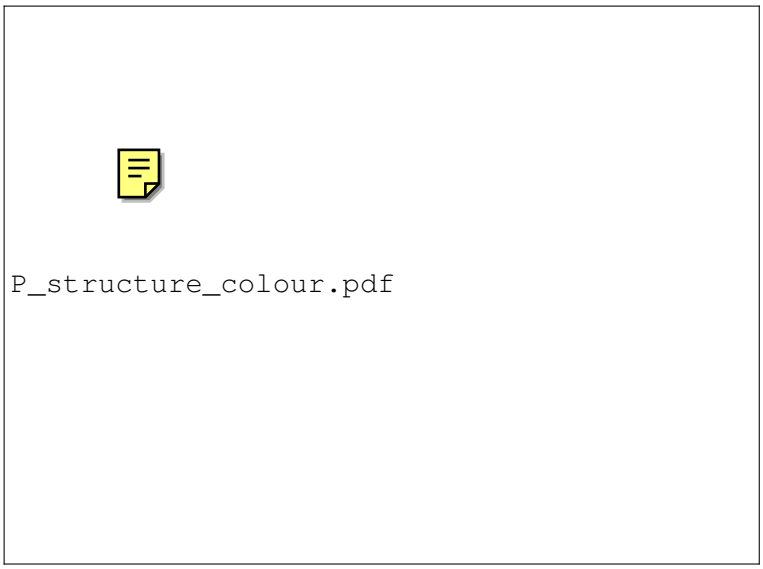

Figure 7: Phytochrome configuration change from P_r (left) to P_{fr} (right). Photoconversion of the chromophore involves a cis/trans isomerisation. Changes in conformation of the apoprotein are a consequence of the photoconversion of the chromophore. Modified from Mohr and Schopfer (1995)

mophore/protein configuration (Fig. 7). These two forms have distinct light absorption spectra (Fig. 8) with absorption maxima in the red (P_r) and far-red (P_{fr}) regions of the spectrum. Interconversion occurs as a result of light absorption: $P_r \rightleftarrows P_{fr}$. During this photo-conversion short lived intermediates appear. Breakdown (or 'destruction') of P_{fr}, and dark reversion also occur, but at lower rates than photo-conversion.

$$\xrightarrow[{}^{0}k_s]{\text{synthesis}} \boxed{P_r} \underset{\lambda_{730}\ \text{dark}}{\overset{\lambda_{660}}{\rightleftarrows}} \boxed{P_{fr}} \xrightarrow[{}^{1}k_d]{\text{breakdown}}$$

Phytochrome is synthesised as P_r, while the biologically active form is P_{fr}. The path from P_{fr} to a plant photoresponse involves a *signal transduction chain*, and competent cell functions. An example of a function competent for P_{fr} is the promotor region of some genes.

As the absorption spectra of P_r and P_{fr} overlap, a *photoequilibrium* is reached depending on the wavelength of monochromatic light, or the spectrum of polychromatic light, when fluence is saturating, but irradiation time short. For longer irradiation times and relatively high irradiance, the size of the total P pool ($P_r + P_{fr}$) depends on the rates of synthesis and breakdown. When both rates are equal, and so they cancel each other, a *photo-steady state* is reached. These different states are reflected in the different modes of action of phytochromes.

The responses mediated by phytochromes have been classified into three *modes of action* depending on their light exposure requirements: *high irradiance responses* (HIR), *low fluence responses* (LFR), and *very low fluence responses* (VLFR) (Fig. 9). VLFR has been reported in seeds that do not germinate in darkness but for which germination can be induced by extremely

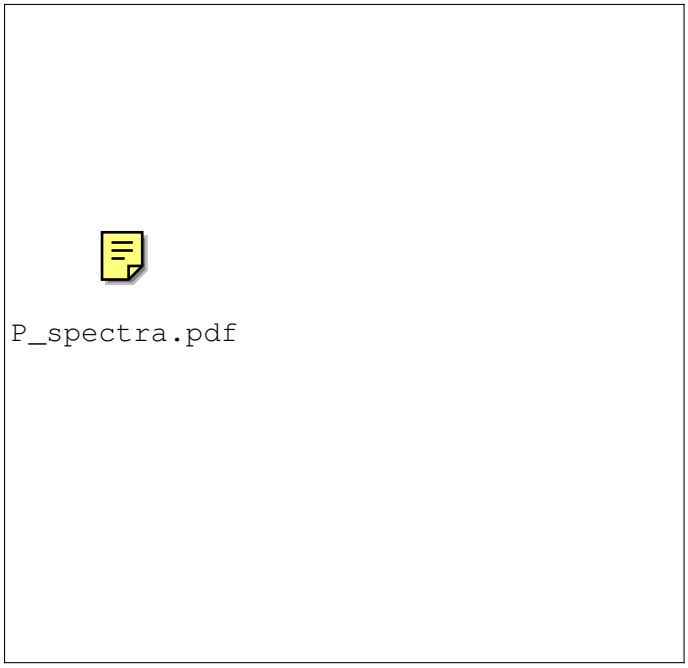

Figure 8: Absorbance spectra of phytochrome *in vitro*. Spectrum for P_{fr} (broken line) was calculated from the spectrum measured under red irradiation (80% P_{fr}) and that measured under far-red irradiation (99% P_r). The upper curve shows the difference in absorbance between P_r and P_{fr}. From Mohr and Schopfer (1995)

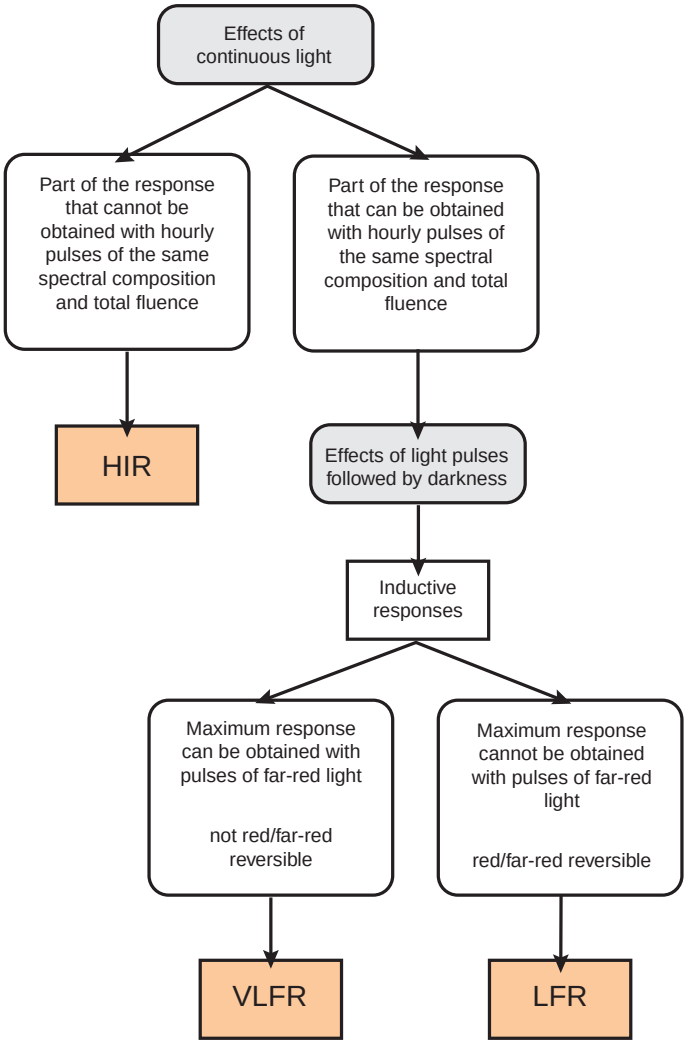
Effects of continuous light
Part of the response that cannot be obtained with hourly pulses of the same spectral composition and total fluence
Part of the response that can be obtained with hourly pulses of the same spectral composition and total fluence
HIR
Effects of light pulses followed by darkness
Inductive responses
Maximum response can be obtained with pulses of far-red light
not red/far-red reversible
Maximum response cannot be obtained with pulses of far-red light
red/far-red reversible
VLFR
LFR

Figure 9: Plant responses mediated by phytochrome: operational criteria for *modes of action*. Redrawn from Casal et al. (1998)

brief pulses of white light such as during soil tillage, or in the laboratory by FR. LFR is the most usual, and first described, phytochrome-dependent response. There are many examples of responses to R pulses reversible by a subsequent FR pulse. For example, germination promoted by R and inhibited by pulses of FR (Or in a few cases the opposite, but always photo-reversible behaviour: germination induced by FR and inhibited by R). HIR, is a response to long exposure to FR which cannot be achieved by several shorter pulses of equal total fluence, and is not photo-reversible. The inhibition of seed germination, and the promotion of anthocyanin accumulation in small seedlings by continuous FR, are two examples of HIR action.

Different phytochromes share the same chromophore, but have differences in the amino acid sequences of the apoproteins. The following symbols and abbreviations are usually used: phyA, phyB... for the different phytochrome species (apoprotein + chromophore); PHYA, PHYB... for the apoproteins; *PHYA*, *PHYB*... for the genes encoding them; and *phyA*, *phyB*... for the non-functional mutant alleles of these genes. The number and *type* of phytochrome encoding genes is different in the plant species for which comprehensive information is available. In *Arabidopsis thaliana* there are five genes encoding for phytochrome apoproteins: *PHYA* through *PHYE*. In tomato there are also five: *PHYA*, *PHYB1*, *PHYB2*, *PHYE*, and *PHYF*. According to their sequences, there are three lineages of phytochrome genes in flowering plants: *PHYA*, *PHYB/D/E*, and *PHYC/F* (Mathews and Sharrock, 1997). phyA is the most abundant phytochrome in etiolated[2] angiosperm seedlings, but under red or white light its P_{fr} form is proteolytically degraded. The other phytochromes (called 'stable' phytochromes) predominate in light grown plants. As P_{fr}A and P_{fr}B differ in their stability, abundance of phyA varies following a diurnal cycle, but not that of phyB. Abundance of different phytochromes also varies with the tissue and ontogeny (e.g. phyA is most abundant in root tips in tomato seedlings Pratt et al., 1997).

Different phytochromes have different functions in the plant —i.e. they are active at different ontogenic stages, or control different responses, or are involved in different modes of action (Table 2). This is a very active field of research at the moment, and fast progress has been possible using apoprotein deficient mutants, and transgenic plants (both sense and antisense). These techniques make it possible to experimentally manipulate the concentrations of individual phytochromes. The latest, and very exciting achievement, has been the overexpression of *PHYA* targeted to certain plant organs.

3.2 Blue/UV-A photoreceptors

Blue/UV-A photoreceptors are present in many different organisms: bacteria, fungi, green plants, and animals. For many years the only proof of their existence in plants was the sensitivity of plants to light in the blue/UV-A region of the spectrum, and because of the difficulty in isolating these pigments the name cryptochrome originated (crypto = hidden). However, although *cryptochrome* was used for many years as a generic name for all putative pigments with high absorption of blue and ultraviolet-A radiation, nowadays this name is used only for members of the family of blue/UV-A photoreceptors whose chemical identity was described first.

In recent years it has become evident from spectral and genetical evidence that there are at

[2]Etiolated = grown in darkness.

Table 2: Responses mediated by phytochromes in angiosperms. + indicates response, − opposite response, 0 no effect, ? unknown effect, ( ) indirect effect (e.g. modulation of response amplitude). An effect in the column 'phyC–E' means that at least one of phyC, phyD and phyE is involved in the response (i.e. the phyA/phyB double mutant shows a response). This is a tentative classification only, based mainly on data from *Arabidopsis thaliana* and some *Solanaceae*. phyA–E are the phytochromes present in Arabidopsis, there is variation in the number and 'type' of phytochrome genes depending on the species.

	phyA	phyB	phyC–E	reference
VLFR	y	n	n	Whitelam and Devlin, 1997, and refs.
LFR	n	y	y	Whitelam and Devlin, 1997, and refs.
HIR	y	n	n	Whitelam and Devlin, 1997, and refs.
end-of-day FR	n	y	y	Whitelam and Devlin, 1997, and refs.
night break FR	y	n	n	Whitelam and Devlin, 1997, and refs.
germination	+	+|−	+	Whitelam and Devlin, 1997, and refs.
stem extension[a]	0|+	+	0	Casal et al., 1997
stem extension[b]	+	(+)[c]	0	Casal et al., 1997
hypocotyl exten.[d]	+	+	?	Whitelam and Devlin, 1997, and refs.
leaf expansion	0	0	+	Qin et al., 1997
root growth	+|?	+	?	Kurata and Yamamoto, 1997
elong. root hairs	?	+	?	Reed et al., 1993
de-etiolation	+	+	?|0	Yanovsky et al., 1995; J. J. Casal, pers. com.
flowering	+	−	−	Devlin et al., 1999; Whitelam and Devlin, 1997, and refs.
tuberization	?	−	?	Jackson et al., 1998
phototropism	(+)	(+)|+	?	Ballaré, 1999; Hangarter, 1997

[a] 'Shade avoidance' in de-etiolated plants.
[b] 'Neighbour detection' before shading in de-etiolated plants.
[c] Only in combination with phyA
[d] In etiolated seedlings.

least three groups of blue/UV-A photoreceptors: the flavoproteins called *cryptochromes* (CRY1, CRY2 and CRY3 in *Arabidopsis*) and *phototropins* (PHOT1 and PHOT2 in *Arabidopsis*), and possibly a photoreceptor with the carotenoid xanthophyll as chromophore (Horwitz and Berrocal, T, 1997). There are additionally some recently identified receptors, mostly involved with flowering induction and circadian rhythms (endogenous clock): ZTL/FKF1/LKP2 family (Banerjee and Batschauer, 2005, and references therein).

Initially, one cryptochrome was unequivocally characterised as a flavoprotein by Ahmad and Cashmore (1993). Later it became evident that a family of flavoprotein photoreceptors exists in arabidopsis: CRY1 and CRY2 (Cashmore, 1998). These cryptochromes have dual chromophores: FAD (flavin adenine dinucleotide), and a deazaflavin or a pterin. Their apoprotein of XXXkD has similitude to photolyases, but no DNA-repair activity. These flavoproteins are involved in photomorphogenesis, photoperiodism and possibly phototropism (Table 3). Responses mediated by CRY1 and CRY2 are relatively slow, taking at least several hours to be detected. They can be localized in the nucleus and mediate gene induction by blue light (Ohgishi et al., 2004). Cryptochromes differ in their photostability being CRY1 more stable than CRY2. Because of this, it has been suggested that CRY2 has an important role only under low fluence. In the same way as different phytochromes have different functions in the plant, CRY1 and CRY2 also differ in their functions in the plant. However, sometimes they can substitute for each other as in the case of phototropism —i.e. only the double mutant differs in phenotype from the wild type. (Table 3).

Although other photoreceptors affect phototropism, phototropins (PHOT1, and PHOT2; PHOT1 formerly called NPH1, PHOT2 formerly called NPL1) are the main photoreceptors involved in phototropism in response to blue light, as the *phot1* mutant of *Arabidopsis* has no phototropic response to blue light (see Briggs and Christie, 2002, and references therein). PHOT1 is a membrane bound flavoprotein of 120 kD and has FMN (flavin mononucleotide) as chromophore (Christie et al., 1998). Other relatively fast responses like stomatal opening in response to blue light, and movement of chloroplasts are also mediated by phototropins. However, there is an additive effect of CRY1 and CRY2 in the case of stomata —apparently with phototropins alone mediating opening at low levels ($< 5\ \mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$) of blue light, and both families of photoreceptors involved at higher irradiances (Mao et al., 2005). The involvement of cryptochromes in stomatal opening under blue light was observed in experiments using a background illumination with red light. Phototropism under low light levels (or light pulses) seems to be mediated by PHOT1, while phototropism under high light levels seems to be mediated by PHOT2 (Briggs *et al.*, 2001, and references therein). PHOT1 and PHOT2 are not evenly distributed in the plant: in rice PHOT1 predominates in coleoptiles while PHOT2 predominates in leaves (Briggs *et al.*, 2001). Phototropins mediate in general fast responses that can be detected in less than an hour. The induction of very few genes by blue light seems to be mediated by PHOT1 or PHOT2 (Ohgishi et al., 2004). PHOT1 is localized to the plasma membrane region, but is partly released to the cytoplasm by blue light (Sakamoto and Briggs, 2002), and mediates the activation of calcium-permeable channels by blue light (Stoelzle et al., 2003).

In the case of stomatal guard cell responses to blue light there is some evidence suggesting that one of the photoreceptors involved has the carotenoid xanthophyll as chromophore (Zeiger and Zhu, 1998)(Table 3). Additionally this type of photoreceptor could be involved in the control

Table 3: Responses mediated by blue/UV-A photoreceptors. Cryptochromes: CRY1, CRY2; phototropins: PHOT1, PHOT2. + indicates enhanced response by blue or UV-A light, − depressed or suppressed response, 0 no effect, ? unknown effect, ( ) indirect effect (e.g. modulation of response amplitude). This is a tentative classification only, based on data from *Arabidopsis thaliana* mutants. (See also Table 1 in Banerjee and Batschauer, 2005 and references therein).

	CRY1	CRY2	PHOT1	PHOT2	zeaxanthin	reference
germination	?	?	?	?	?	
cotyledon expan.	+	?	+	+	?	Ohgishi et al., 2004
hypocotyl exten.	−	−	0	0	−	Lascève et al., 1999
anthocyanin	+	?	?	?	?	Batschauer, 1998, and refs.
CHS expression	+	+	?	?	?	Batschauer, 1998, and refs.
de-etiolation	+	?	0	0 ?	?	Batschauer, 1998, and refs.
flower induction	0 ?	+	0	0 ?	?	Batschauer, 1998, and refs.
phototropism	(+)	(+)	+	+	0	Lascève et al., 1999
chloroplast mov.	0	0	+	+	?	Briggs *et al.*, 2001, and refs.
stomatal opening	+	+	+	+	+ ?	Lascève et al., 1999; Mao et al., 2005, and refs.

of hypocotyl extension (Lascève et al., 1999).

So several different families of blue/UV-A photoreceptors have been identified, and when interpreting experimental results this and the fact that phytochromes do have a minor absorbtion peak in this region of the spectrum should be taken into account. In contrast to what happens with the red/far-red reversibility of response in the case of the LFR through phytochromes, there is no physiological means of identifying other photoreceptor involvement. It is necessary to rely on well characterised genotypic differences to establish photoreceptor involvement.

3.3 UV-B photoreceptor(s)

There is some evidence suggesting that responses to ultraviolet-B radiation are caused not only by damage (e.g. to DNA) but also by perception through a photoreceptor. A photoreceptor distinct from CRY1, at least in the case of *CHS* transcription (e.g. Jenkins, 1997). Recent evidence suggests that there may be two different photoreceptors involved with separate signalling pathways, one active in the short-wavelength UV-B (280–300 nm) and another one active in the long-wavelength UV-B (300–320 nm) (see Ulm and Nagy, 2005, and refs. therein). HY5 seems to be involved in the transduction leading to some photomorphogenic responses to UV-B. HY5 is also known to be involved as a regulator in responses mediated by phytochromes and cryptochromes.

It has been suggested that the UV-B photoreceptor is also a flavoprotein (Ballaré, Barnes and

Flint, 1995). The only evidence available at the moment is (1) that effects of UV-B can be observed at very low fluence, before any 'damage' is apparent, (2) some of these responses can be blocked by an inhibitor. Other possibilities are that products of DNA damage, or oxidative stress itself are sensed.

3.4 Other photoreceptors

An unusual photoreceptor with features in common with both phytochromes and phototropin has been characterised in the fern *Adiantum* (Nozue et al., 1998). The fusion of a functional photosensory domain of phytochrome with a nearly full-length phototropin (PHOT1) homolog suggests that this polypeptide could mediate both red/far-red and blue-light responses in *Adiantum* normally ascribed to distinct photoreceptors in other plants.

Although there is no compelling evidence at the moment, the existence of other photoreceptors in plants has been suggested (e.g. heliochrome, a supposedly green/far-red photoreversible pigment involved in HIR, Tanada, 1997). Moreover, the possibility of finding in the future new photoreceptors, or pigments related to those currently known for other groups of organisms clearly exists, as the recent identification of a CRY1-like gene in humans and animals demonstrates (Cashmore, 1998).

3.5 Interactions

There is light-dependent epistasis among certain photoreceptor genes because the action of one pigment can be affected by the activity of others. Complex interactions exist, and several plant responses to light depend on the concurrent activity of different photoreceptors: e.g. phytochrome B, cryptochromes and phototropin for phototropism, or phytochrome A and phytochrome B for responses to far-red light reflected by neighbours. Earlier interactions among wavebands have been described. One physiologically well studied example is the metabolism of phenolics (see section 5.4), but more recently other interactions have been characterised using mutants (see Casal, 2000, for details).

We will follow Casal (2000) and use *synergism* and *antagonism* to describe the interaction between gene products, not the mutations themselves. We will take the de-etiolation of *Arabidopsis thaliana* seedlings as an example. Casal (2000) describes the response in more detail.

A single pulse of red light is not fully effective to initiate de-etiolation. One of the photoreceptors that mediate de-etiolation is phyB. Under white light, de-etiolation is partly impaired in the *phyB* mutant. However, although a single pulse of red light per day transforms phyB to the P_{fr} (active) form some of the de-etiolation responses (e.g. hypocotyl growth inhibition) are not obvious. Four conditions have been identified where the pulse of red light perceived by phyB does induce these responses: (1) in the absence of phyA (i.e. *phyA*-mutant background); (2) when the seedlings are previously exposed to far-red light perceived by phyA; (3) when the seedlings are previously exposed to blue light perceived by cry1 and (4) when the seedlings are previously exposed to UV-B radiation. These conditions define photoreceptor interactions.

(1) The interaction between phyA and phyB is antagonistic. phyB is somewhat impaired by the activity of phyA in the wild type, although phyA itself has some direct contribution to de-

etiolation.

(2) If a daily exposure to FR of 1–3 h is followed by a red light pulse de-etiolation is significant, while the exposure to 1–3 h of FR is not[3]. The red light pulse has no effect in the *phyB* mutant, while the *phyA* responds in the same way to the red light pulse with or without the FR pretreatment. The interaction between phyA and phyB is in this case synergistic.

(3) Exposure to blue light is also able to induce the response to a red pulse. This reponse is deficient in both the *phyB* and *cry1* mutants. This interaction is also synergistic.

(4) Short exposure to UV-B at low irradiance can have photomorphogenic effects. The photomorphogenic effect (e.g. cotyledon unfolding) is observed if the UV-B exposure is terminated with a pulse of red light but not if terminated with a pulse of far-red light. The first condition is not effective in *phyB*-mutant seedlings. This is a synergistic interaction between phyB and an unidentified UV-B photoreceptor.

Furthermore, the relative importance of different photoreceptors, and transduction chains, can depend on developmental stage and tissue considered (Schafer et al., 1997). Also environmental conditions like ambient temperature and photoperiod can differently affect the different phytochromes and/or their transduction chains (Halliday and Whitelam, 2003).

4 Cellular transduction chains

Knowledge of the transduction chains involved in responses to light is patchy. Methods from molecular biology are currently being used to dissect these chains, but they are complex and branched (i.e. using mutants it has been observed that different responses share only some initial steps in the transduction chain, or even that the same response when driven by VLFR and HIR depends on partly different chains). For this reason only a few examples are given here.

P_{fr}, the active form of phytochrome, affects protein biosynthesis through activation of DNA transcription factors. Activation factors are frequently proteins that are activated or deactivated by phosphorylation catalysed by protein kinases. For the induction of greening in etiolated seedlings there is evidence of the participation of Ca^{2+} and calmodulin. In the case of chalcone synthase cGMP seems to be involved. In both of these transduction chains a G-protein is probably involved. These *G-proteins* or *GTP binding proteins* are part of transduction chains in both animals and plants.

P_{fr} has multiple effects: for example, in mustard cotyledons gene expression is altered so that phenylalanine ammonia lyase (PAL) is induced, lipoxygenase synthesis is stopped, and isocitrate lyase is not affected. Signal transduction from the cytosol to promotors in the nucleus remains partly unknown. Certain regulatory DNA sequences (cis-trans acting elements) are necessary for the effects of light to take place.

Recent experiments show that phyB binds photoreversibly to PIF3, a nuclear basic helix-loop-helix protein (Ni et al., 1999). PIF3 is a putative transcriptional regulator providing a potential mechanism for direct photoregulation of gene expression.

All five phytochromes in *Arabidopsis* migrate to the nucleus and the import to the nucleus is regulated by light, but differently for the different phytochromes (Kircher et al., 2002). In the

[3] Continuous FR, or longer daily exposures are effective.

nucleus phytochromes form speckles, which are apparently functionally important.

5 Whole plant responses to light

Whole plant responses to spectral light quality and irradiance are numerous. Four examples are described in some detail in the following subsections: (5.1) Control of seed germination by light perceived through phytochromes. (5.2) Changes in leaf area expansion and leaf morphology in response to end-of-day pulses of red and far-red light. (5.3) Accelerated stem elongation in response to increased far-red irradiance in the horizontally propagated light. (5.4) Increased synthesis of phenolics induced by ultraviolet-B and modulated by red:far-red photon ratio. Many other responses have been described, several of them are common examples in text books (e.g. Attridge, 1990; Mohr and Schopfer, 1995; Taiz and Zeiger, 1998).

5.1 Seed germination

Phytochromes are involved in the sensing of the light environment by seeds, and the control of germination by red and far-red light was one of earliest phytochrome-mediated responses described (see Casal and Sánchez, 1998). All three modes of action (VLFR, LFR, and HIR, see Fig. 9 and section 3.1 on page 14) have been described in seeds. phyB is present in dry seeds while phyA appears after imbibition. phyA mediates VLFR, while phyB and the other phytochromes mediate LFR. phyA is also probably responsible for HIR.

Phytochromes can affect the growth capacity of the embryo and/or the constraint imposed by seed tissues around it. Experimentally this can be tested by measuring the germination of intact vs. decoated seeds, and isolated embryos vs. embryos in seeds. Seed coats not only create a mechanical obstacle for growth, but also filter the light changing the quality of the light reaching the embryo. Plant hormones such as gibberelins, and cytokinin could be involved in the transduction chain.

Seeds of numerous plant species require light for germination. In most cases a pulse of red light induces germination compared to darkness, and a subsequent pulse of far-red light *reverts* the effect of red (a LFR response). Depending on the phytochrome equilibrium in the seeds, which depends on earlier exposure to light (e.g. inside the green fruit) a far-red light pulse can inhibit germination in comparison to darkness. The phytochrome pool involved in LFR is relatively stable, and it can remain active for at least 2 d (this has been tested with seeds that require and additional condition for germination, for example alternating temperatures, by delaying the fulfilment of this second requirement after applying the inductive light treatment). P_{fr} is not totally stable, as dark reversion to P_r occurs, and can be seen in this type of experiments when the initial photoequilibrium is established with a mix of red and far-red light instead of pure red.

In some species, usually after a certain pretreatment like burial in the soil, seed germination can be induced by very brief pulses of light. In this case both red and far-red light increase germination. It is possible that different transduction chains are involved in LFR and VLR for the same response. Continuous far-red light through HIR is the mechanism behind inhibition of seed germination by continuous light that is observed in some species.

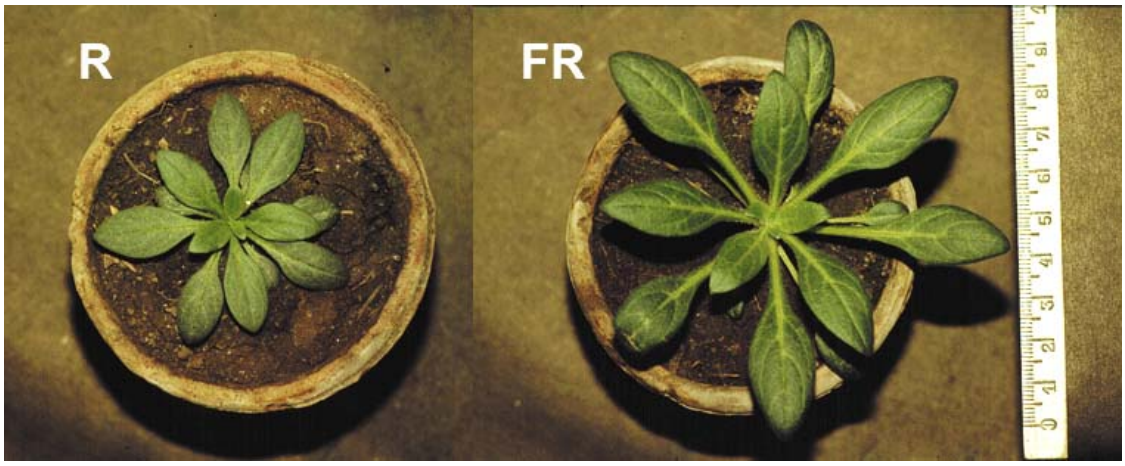

Figure 10: Plants of *Petunia axillaris* grown under a short days regime and briefly irradiated at the end of the photoperiod with either red light (R) or far-red light (FR). Ruler marked in centimetres. From Casal et al. (1987)

5.2 Size and shape of leaves

A rather un-natural but effective manipulation of the light environment is to subject plants to brief (5 to 15 min) pulses of red or far-red light at the end of the photoperiod[4]. Recent studies have shown that responses to this kind of treatments are mediated by phytochromes other than phyA.

In *Petunia axillaris* leaf expansion under equal photon irradiance was greatly enhanced by an end-of-day far-red light pulse compared to a red light one (Fig. 10). The chlorophyll concentration per unit dry weight and per unit leaf area concurrently decreased. The effect of a FR pulse is reverted if followed by a R pulse (Casal et al., 1987). In *Petunia axillaris*, which is a plant with a rosette growing habit and does not elongate the stems in response to far-red light, the positive effect on leaves is especially clear. The different behaviour of rosette plants and those with elongated stems is caused by different constraints in the allocation of a limited pool of photo-assimilates.

In many species the shape (e.g. length to breadth ratio) changes in response to irradiance, but light quality can also have a dramatic effect. For example in *Taraxacum officinale*, another species with a rosette growing habit, an end-of-day far-red light pulse not only increases the length to breadth ratio, but also inhibits the development of runcinate leaves[5] (Sánchez, 1971).

In *Fuchsia magellanica* the interaction between the effects of photosynthetically active irradiance during the photoperiod and light quality at the end-of-day was studied. Both factors had a notable effect, but the effect of light quality was mainly on internode length and branching angle, not on leaf area (Fig. 11). In *Betula pendula* seedlings additional lateral far-red light had no effect on leaf area per plant, but a significant effect on height growth (P. J. Aphalo and T.

[4] *Photoperiod* is the daily period with illumination, usually expressed in hours.
[5] *Runcinate* leaves have teeth as opposed to leaves with entire margins.

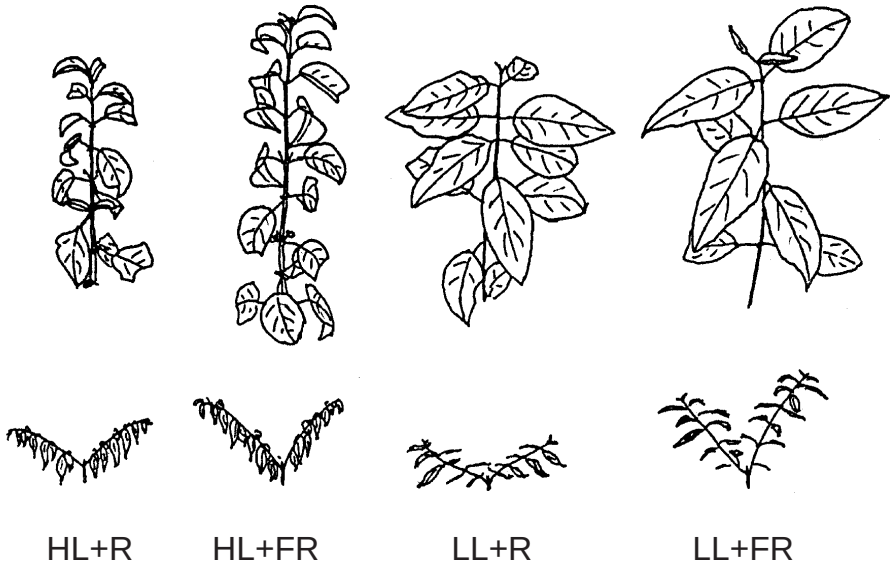

Figure 11: Plants of *Fuchsia magellanica* grown under a short days regime under two irradiances: 450 μmol m^{-2} s^{-1}, HL, and 30 μmol m^{-2} s^{-1}, LL, and irradiated for 10 min at the end of the photoperiod with either red light (R) or far-red light (FR). Experiment and results described by Aphalo et al. (1991)

Lehto, unpublished). In many other species (e.g. *Nicotiana tabacum*, *Cucurbita pepo*, *Sinningia speciosa*, *Chenopodium album*, *Rumex obtusifolius*), in which far-red causes a large increase in stem elongation, leaf area is decreased by this same treatment (see references in Casal et al., 1987).

One very important consequence of plants having thinner and larger leaves when shade adapted is that, because these changes increase photosynthesis per unit leaf dry mass, they increase plant relative growth rate compared to non-shade adapted plants. Thinner leaves also result in lower respiration rates per unit leaf area. Changes in the size and shape of leaves (e.g. entire margins instead of runcinate leaves) directly affect boundary layer conductance, and indirectly water and energy exchange.

5.3 Stem elongation

As described in section 2.2, far-red light reflected by neighbouring plants (or neighbours for short) decreases R:FR in horizontally propagated light, as 'seen' by vertically oriented plant surfaces (see Aphalo and Ballaré, 1995). This happens at low canopy densities, so it is especially important for small seedlings in sparse canopies.

The stems of many plants elongate faster if they receive additional far-red light from the side (see Ballaré, 1999, and references therein). In general, the magnitude of the response to far-red light depends on the species, developmental stage, and other environmental variables such as blue light and/or photosynthetically active irradiance incident on the leaves. However, at low canopy densities there is no actual shading of leaves by neighbours.

When measured under laboratory conditions, the stem elongation response to far-red light incident on the stem can be shown to have a very short lag (of the order of minutes in small seedlings) but continue for some time after the end of the stimulus (Casal and Smith, 1988a,b).

The photoperception of the lateral far-red light takes place in the growing internodes. In sparse canopies, the perception of neighbours is mediated mainly by phyB and probably sensitivity is modulated by phyA[6].

5.4 Metabolism of phenolics

Anthocyanin synthesis is a common response to light in many seedlings and is also present in some non-juvenile plants (see Mohr and Schopfer, 1995). Anthocyanin is regarded as a protective pigment, shielding light sensitive porphyrins in greening tissues. In mustard (*Sinapis alba*) seedlings induction of anthocyanin synthesis in cotyledons occurs exclusively via phytochrome. The amount of anthocyanin follows closely the P_{fr}/ P_{tot} ratio. Control seems to occur in two stages: (1) coarse regulation, by induction of two key enzymes of flavonoid metabolism, PAL (phenyl-alanine ammonia lyase) and CS (chalcone synthase) by P_{fr}; and (2) fine regulation by post-translational control, also by phytochrome.

It has been suggested that phytochrome is the main effector and that cryptochrome and the UV-B receptor modulate the sensitivity of photoresponses to P_{fr} (see Mohr and Schopfer, 1995).

[6] At high canopy densities, presumably phyE and phyD play an important role, but not in the detection of reflected far-red light in sparse canopies

There is evidence for this in some systems like anthocyanin accumulation in *Sorghum bicolor* seedlings were R and FR have no effect without pre-irradiation with B and/or UV-A. For inducing synthesis of anthocyanins in the coleoptiles of wheat (*Triticum eastivum*) R, FR, blue and UV-A are ineffective without a (low irradiance) background of UV-B. In wheat again anthocyanin synthesis is controlled by P_{fr} after irradiation with UV.

Frequently, to obtain the full photoresponse by P_{fr}, also absorption of light by cryptochrome is needed. In de-etiolated Scots pine (*Pinus sylvestris*) seedlings R and FR have no effect on hypocotyl elongation in absence of blue light, but have a strong effect when blue is present as background illumination. In light grown *Fuchsia magellanica* plants, anthocyanin synthesis is enhanced by end-of-day R, but only in plants that grow under relatively high white light irradiance (Aphalo et al., 1991).

In cell suspension cultures of parsley (*Petroselinum hortense*), flavone glycosides are formed under UV illumination (peak $\approx 300nm$, in the UV-B region). Visible light is almost ineffective. The UV used has no detrimental effect on growth, this is a positive effect of UV (Wellman, 1975). The law of reciprocity holds and the amount of flavonoids formed is proportional to the amount of UV. Again after irradiation with UV, P_{fr} regulates flavonoid synthesis, but without pretreatment R and FR pulses are ineffective. There is a four times increase in PAL amount after UV + R, but only a very small effect of UV + far far-red light.

6 Plant populations and their ecology

In the previous section examples of how light quality can affect the growth and metabolism of individual plants were presented. In this section examples of how light quality can affect, either directly or indirectly, plant-plant interactions will be discussed. The importance of these effects on canopy or stand behaviour are briefly discussed. The following four examples are presented: (1) How plants synchronise their development to seasonal and stochastic changes in their environment. (2) How plants find and colonise gaps in canopies. (3) How plants adjust the root:shoot balance. (3) How plants avoid being overtopped by neighbours.

6.1 Timing and location

Timing of development and of hardening and dehardening in relation to the seasons of the year is crucial in most regions of the world, but this synchronisation of the activities of plants is most dramatic and easier to observe at high latitudes. In addition to timing in relation to seasons, timing in relation to disturbances is also important (e.g. gap formation in forests, tillage in agroecosystems for seed germination). In the first case photoperiodic responses, mediated by night length sensing through phytochromes and CRY2 are very important, but sensing of temperature is also involved. In the second case both sensing of shade (by phytochrome through LFR and possibly HIR) and amplitude of variation and mean daily temperature are very important. In the case of seeds location at the soil surface, or depth in the soil profile are sensed.

Flowering is in many species induced by either short or long days, with the threshold for induction varying between populations of the same species adapted to growth at different latitudes.

Figure 12: Silver birch tree (*Betula pendula*) growing at the campus of the university of Joensuu. The leaves near the street lamp, which is on throughout the night, turn yellow and drop about one week later than those in the rest of the tree.

In trees from high latitudes (e.g. silver birch, Scots pine), growth cessation and formation of winter buds is triggered by short days. The day-length threshold for growth cessation depends on the latitude of origin of the population. Leaf senescence seems to be mainly controlled by low temperatures but is further modulated by photoperiod (Fig. 12).

Seed germination is usually controlled by a complex combination of environmental factors. In general, the behaviour of seeds stored in the laboratory and those remaining in their natural habitat is different. Seeds buried in the soil tend to display seasonal variations in their readiness for germination (e.g. light and temperature requirements change). From the adaptive point of view, this complex sensory mechanisms ensure that germination occurs at the right time of the year and under favourable conditions for seedling establishment. Some responses of seeds of some weeds of field crops, seem to have evolved under cultivation, and allow seeds to sense tillage operations through sensing of very brief light pulses (phytochrome through VLFR). In practice this can be demonstrated by the, sometimes large difference, in the germination of weed seeds in fields ploughed during day- and nighttime (or experimentally at night with and without artificial light).

6.2 Searching for light

Phototropism is the growth towards the light. Growth away from neighbours has also been demonstrated. A related phenomenon is the *patterning* of leaf display which reduces shading between adjacent leaves. Increased apical dominance and changes in branch and tiller insertion angle towards the vertical also may improve access to light.

In de-etiolated plants, phototropism is a response to both blue/UV-A and far-red light Ballaré (1999) . Neighbour avoidance and the growth towards gaps in green canopies, is a response at least in cucumber, partly mediated by phyB Ballaré et al. (1995). We know very little about the mechanisms behind leaf patterning, but in cucumber leaf display angle is altered in a *phyB* mutant. Increased apical dominance and more vertical stems or tillers is a frequent response to end-of-day FR (Fig. 11) or daytime low red:far-red photon ratio. It is not yet as clearly demonstrated as for height growth, but it is very likely that plants are also able to partly avoid neighbours by sensing FR and modulating radial (i.e. lateral) growth before actual shading takes place.

6.3 Light quality, roots and mineral nutrients

Light quality (and irradiance) incident on shoots can affect the growth of roots by indirectly affecting the photosynthate availability in roots, either because of changes in allocation or changes in assimilation. In turn changes in the root growth, morphology and symbioses can affect the ability of plants to take up nutrients form the soil. More directly, light quality can affect the metabolism of enzymes involved in nitrogen metabolism. At the biochemical level light dependent light induction and modulation of enzyme activity has been studied in some detail. On the other hand, effects of light quality on whole plant mineral nutrient uptake and status have been little studied.

In some cases decreased R:FR has decreased root growth compared to shoot growth, however this is not always the case, as sometimes, especially in woody plants, stems elongate without increasing their dry weight (they are longer but thinner).

In soybean (*Glycine max*) plants end-of-day far-red treatment decreased the number of nitrogen-fixing root nodules per plant (plant-bacterial symbiosis with *Rhizobium*) (Kasperbauer et al., 1984). In *Pinus sylvestris* seedlings, additional lateral far-red light decreased the size of the root system, and the number of ectomycorrhizas per plant, but not the number of mycorrhizas per unit root length (de la Rosa et al., 1998).

The concentration of nitrogen in leaf, and sometimes stem, tissues can be higher in plants receiving additional far-red light (Aphalo and Lehto, 1997; de la Rosa et al., 1998).

As discussed above, light quality may affect the mineral nutrient uptake and assimilation capacity of plants. The complementary question is: can mineral nutrient availability affect responses to light quality? In *Betula pendula* seedlings a moderate and short term limitation of nutrient supply does not seem to affect responses to far-red light (Aphalo and Lehto, 1997, P. J. Aphalo and T. Lehto, unpublished). In *Pinus sylvestris* seedlings a more drastic and long lasting limitation in nutrient supply has been suggested to inhibit shoot responses to lateral far-red (de la Rosa et al., 1998, 1999). This was interpreted as a switch of strategy from competition for light to competition for nutrients, as the N and P contents were higher in far-red treated plants under conditions of low availability of nutrients.

6.4 Being good neighbours

Plants in nature, or under cultivation, rarely grow isolated. They grow together with other individuals of the same and/or other species forming a canopy. Many environmental variables vary with the density and or position in a canopy (Aphalo and Ballaré, 1995), and could provide valuable information to plants for adapting to the particular situation. Probably the most important of these informational signals are conveyed by light (Aphalo et al., 1999). As we have seen above, plants growing near other plants (neighbours) that reflect far-red light grow taller than if they are alone. Furthermore, as the red:far-red photon ratio in horizontally propagated light varies with depth in the canopy, the deeper plants are in the canopy the more intense is the light quality signal they receive. It has long been recognized that the stem and petiole elongation responses to red:far-red photon ratio are related to competition for light and these and related responses constitute a syndrome, usually called "shade avoidance response". More recently it has been demonstrated that plants can perceive neighbours even before actual shading takes place (Ballaré et al., 1987). This perception happens through the increase in reflected far-red light at low canopy leaf area indexes (e.g. less than 1 m^2 of leaf area per 1 m^2 of ground area, see Fig. 6).

If when shaded the shorter individuals grow taller, their share of the light resource improves and consequently the intensity of asymmetrical competition for light decreases. By reducing differences in height among individuals, shade-avoidance indirectly reduces the variation in growth rate, size and reproductive output. Reducing size inequalities improves whole canopy performance because individuals which die before reproduction, or produce a meagre yield of propagules, have captured resources (mineral nutrients, water and light) early in the season making them unavailable to the successful individuals which later on out-competed them. With large enough size inequalities among individuals the resources available for reproduction and growth are partly "wasted" decreasing the efficiency of their use by the canopy as a whole.

Consequently, when looked at from the viewpoint of canopy productivity new aspects of the shade-avoidance response come to light, as summarised by Aphalo et al. (1999):

- [In monospecific canopies] higher canopy-level productivity is associated with reduced size inequality among neighbours.
- Apparently, for high population-level reproductive output at high densities (yield in cultivated stands) it is not as important that the population is composed of individuals with the "right" phenotype for shade conditions as it is that the population is composed of individuals able to dynamically adjust their phenotype as the canopy develops.
- Shade avoidance by shorter individuals **decreases** the relative competitive advantage of the taller ones.
- Shade avoidance by shorter individuals tends to stabilise the size structure of a canopy (i.e. decreases variation in height, dry mass and reproductive output among individuals).
- Phytochrome plays a very important role, but other factors such as light other than red and far-red, wind, temperature, and 'transpiration demand' may be also important in stabilising plant size inequalities in the field.

Another line of inquire has been to test, from the population biology perspective, if shade avoidance is adaptive (Schmitt, 1997).

More recently, a similar test has been done for responses to UV (Weinig et al., 2004). This test showed that accumulation of phenolics has a cost when UV is excluded, but is beneficial in the presence of UV. Furthermore, populations from open and shaded sites differed in the magnitude of the plastic response.

7 The state of our knowledge

There is still a lot that we do not know, and much of what we know about photoreceptors has been elucidated in the last decade. Whole plant responses had been described much earlier, but the physiological mechanisms involved are only now being discovered. Our knowledge is still fragmentary:

- Most of what we know at molecular level is for a handful of species, with most information for the herb *Arabidopsis*
- Little is known about other growth forms such as trees
- Other families such as grasses and conifers have been little studied
- There is some information on ferns, mosses, and fungi
- The role of the different photoreceptors on the competitive ability of plants growing in mono-specific canopies is almost unknown
- The role of the different photoreceptors on the competitive ability of plants growing in the wild is totally unknown
- Generalizations of our current behavioural knowledge to other species is almost impossible, or at least very risky
- There exist many plant species, further research could yield new exciting discoveries (e.g. new photoreceptors)

Modern molecular biology techniques are providing new insights onto photoreceptor physiological functions and transduction chains at a rapid pace. Progress about eco-physiological roles and inter-specific variation has been slower, but this research should also benefit from the use of these same modern techniques used in combination with traditional eco-physiological research methods.

8 Further reading

An out-of-date list of suggested readings and bibliography in plant photobiology is available on line at `http://www.kolumbus.fi/pedro.aphalo/old_pages/pdf/readings.pdf`.

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